The suppression of *Dendroctonus frontalis* and subsequent wildfire have an impact on forest stand dynamics

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Abstract

Question: Interacting disturbance effects from *Dendroctonus frontalis* outbreaks and wildfire are thought to maintain *Pinus* spp. composition in the southeastern U.S. Our objective was to assess forest composition, structure, and succession following the interaction of two frequently occurring disturbance events in southern *Pinus* spp. forests: cut-and-leave suppression, a commonly used means for managing *D. frontalis* outbreaks, and wildfire.

Location: Western Gulf Coastal Plain, Louisiana, USA.

Method: *Pinus taeda* stands with cut-and-leave suppression and subsequent wildfire were compared to stands undisturbed by *D. frontalis* but with the same wildfire events twenty years after *Pinus* spp. mortality. The woody plant community was assessed in three different size classes and used to predict future forest types with the Forest Vegetation Simulator (50 years).

Results: *P. taeda* is the most abundant (> 50%) species of saw- and poletimber-sizes following cut-and-leave suppression with wildfire and in stands only with fire. Using canonical correspondence analysis, vegetation assemblages were primarily explained by slope position and elevation (7.6% variation explained). Fire intensity and stand age also accounted for variance in the ordination (4.4% and 3.1%, respectively). Dominant and co-dominant *P. taeda* forest types were predicted by the model to be the most abundant forest types in each disturbance regime. In addition, new regeneration represents high hazard for future mortality from *D. frontalis*.

Conclusion: Our study demonstrates that cut-and-leave suppression with additional wildfire disturbance maintains *P. taeda* composition, and does not alter forest composition differently from stands receiving only wildfire. As a result, predicted *Pinus* spp. basal area under both disturbances is great enough to facilitate future bark beetle disturbance.

Keywords: Bark beetle; Canonical correspondence analysis; Forest Vegetation Simulator; *Pinus taeda*; Southern pine beetle; Wilderness.

Abbreviations: C-L+fire = Cut-and-leave suppression and additional wildfire; Fire = Untreated controls with wildfire; FVS = Forest Vegetation Simulator.

Nomenclature: USDA NRCS (Anon. 2005).

Introduction

Abiotic and biotic disturbances play a major role in shaping and sustaining forest composition (Pickett & White 1985). Prior to European settlement, *Pinus palustris* savannahs dominated the forest landscape along the coastal plain of the southeastern U.S., and were maintained by frequent fire events (Boyer 1990). However, anthropogenic influences such as fire suppression, land abandonment, urbanization, and timber production (Landers et al. 1995) have shifted forest succession away from *P. palustris* communities to include *P. taeda* and *P. echinata* and various hardwood species (Baker & Langdon 1990). Forest composition along the coastal plain is now dominated by even-aged *P. taeda* forests, which enhances susceptibility and exacerbates further disturbance from the endemic southern pine beetle, *Dendroctonus frontalis*. *D. frontalis* is now the greatest indigenous biotic threat to forest health in the southeastern U.S. (Schowalter et al. 1981).

D. frontalis is an aggressive phloem-feeding bark beetle that attacks primarily mature and over-mature *P. taeda* and *P. echinata* greater than poletimber size ($\geq$ 12.7 cm DBH), and must kill its host to successfully reproduce (Payne 1980). Lack of proactive forest management creates overstocked, stressed stands primed for beetle outbreaks (Schowalter et al. 1981). *D. frontalis* outbreaks often occur every 6 to 12 years and persist for two to three years (Turchin et al. 1999). During outbreak years, extensive *Pinus* spp., mortality is not uncommon, and extensive economic losses occur.

D. frontalis infestations or 'spots' are commonly managed by the USDA Forest Service using two suppression tactics, cut-and-leave and cut-and-remove, to suppress populations and curtail ecological and economic impacts on public lands (Billings 1980). Both techniques fell currently-infested trees plus an area of uninfested *Pinus* spp. around the expanding edge of the infestation. Each tactic disrupts spot growth and interferes with pheromone communication which leads to SPB dispersal

and increased mortality from hot summer temperatures. In cut-and-leave suppression, felled trees are left in the forest because of inaccessibility for timber removal, management restrictions, or saturation of the timber market, whereas in cut-and-remove suppression, cut timber is salvaged and removed from the forest.

The extensive overstory mortality caused by *D. frontalis* and associated suppression opens the forest canopy, influencing light intensity and duration, air and soil temperatures, rain exposure, and humidity (Pickett & White 1985; Phillips & Shure 1990). These changes in microclimate favor early-successional, shade-intolerant species such as *P. taeda*. However, without additional disturbance, mortality to dominant canopy trees can shift forest composition by releasing shade-tolerant species in the understory from competition (Quaterman & Keever 1962). Furthermore, mortality from *D. frontalis* and cut-and-leave suppression result in copious amounts of downed *Pinus* spp. timber on the forest floor, increasing fuel loads and associated wildfire (Addor & Birkhoff 2004). In the Western Gulf Coastal Plain of the southeastern U.S., frequent lightning strikes and dry periods, in conjunction with the added fuel load from *D. frontalis*-caused mortality, exacerbates the ignition and spread of fire. Schowalter et al. (1981) propose the interaction of *D. frontalis* and wildfire disturbance has maintained early-successional *Pinus* spp. forest communities, thereby preventing a shift in forest composition to later-successional, shade-tolerant hardwood communities.

The extent to which large-scale *D. frontalis* suppression events, coupled with subsequent disturbance from wildfire, influences forest composition and succession is not fully understood. Research to date has concentrated on small-scale mortality events caused by *D. frontalis* in *P. taeda*, *P. echinata*, and *P. virginiana*, forest stands, with little attention to subsequent fire disturbance (Balch 1928; Skeen 1976; Harrington et al. 2000; Rantis & Johnson 2002; Duncan & Linhoss 2005). Our objective was to assess the effects of widespread forest disturbance on forest composition, structure, and succession, focusing on cut-and-leave suppression with subsequent wildfire. *P. taeda* plant communities in the Western Gulf Coastal Plain subjected to cut-and-leave suppression and wildfire were compared to plant communities without *D. frontalis* caused mortality and suppression, but with the same wildfire events. We assessed current woody composition, forest structure, and modeled future vegetation data from current forest composition and structure. Ordination was used to examine the influence of environmental factors, disturbance events and environmental variables, on vegetation assemblages.

Because *P. taeda* is an early successional, shade-intolerant species, we hypothesized that its regeneration

is disturbance-driven, and that mortality from cut-and-leave suppression with subsequent wildfire will result in maintenance of the pre-disturbance *P. taeda* forest type. Subsequent wildfire disturbance should reduce competition for new regeneration and prepare adequate seed beds for plant establishment, thereby facilitating regeneration of shade-intolerant *P. taeda*. Stands receiving only wildfire disturbance are also expected to maintain *P. taeda* dominance, but represent higher canopy densities as a result of *P. taeda* planted initially for timber production. We predicted that new *Pinus* spp. regeneration in the cut-and-leave-managed areas will be less of a hazard to future *D. frontalis* outbreaks than pre-disturbance forests and *P. taeda* stands receiving only wildfire because natural regeneration would yield lower *Pinus* spp. densities.

Methods

Site description

Plots were established in Kisatchie Hills Wilderness (Kisatchie National Forest, Natchitoches Parish, LA, USA) in *P. taeda* stands with widespread canopy loss from cut-and-leave suppression and additional wildfire disturbance. Kisatchie Hills covers 3250 ha of *P. taeda*, *P. palustris*, mixed *Pinus* spp. / hardwood, and upland hardwood forest communities. *P. taeda* stands in Kisatchie Hills Wilderness are dominated by gently sloping to steep, well drained and moderately well drained soils that have a loamy surface layer and a clayey and loamy or clayey subsoil. Plots were also established in terrain characterized as moderately steep, somewhat excessively drained and well drained soils that have sandy surface layer and sandy or loamy subsoil (Anon. 1990). Climatologically it is characterized by mean annual maximum temperature of 24.7 °C with a minimum mean temperature of 12.6 °C, and annual precipitation of 1400 mm (Anon. 2001).

Disturbance regimes

In Kisatchie Hills, *D. frontalis*-caused mortality impacted 1590 ha (ca. 49%) of *Pinus* spp. forest in 1984-1985. During that time, 40 cut-and-leave suppression events encompassing 1335 ha (ca. 41%) were used to contain 70 *D. frontalis* spots within the wilderness boundaries (Clarke 1995). Extensive cut-and-leave suppression was used to contain beetle infestations because protocols for suppressing *D. frontalis* outbreaks within wilderness boundaries, areas prohibited of forest management, were not yet established (Anon. 1987).

In 1987, a high-intensity surface fire engulfed

3000 ha within wilderness boundaries, affecting both cut-and-leave suppressed stands and *Pinus* spp. stands undisturbed by *D. frontalis* (Anon. 1987). Furthermore, two additional low-intensity surface fires occurred in March (633 ha) and July (981 ha) of 2000, each encompassing cut-and-leave suppressed stands, undisturbed *P. taeda* stands, and stands previously disturbed by the 1987 wildfire.

In 2004 and 2005, 20 years following the initial disturbance in 1984-1985, we compared forest composition, structure, and succession in *P. taeda* stands (size 4-57 ha) that had been managed for *P. taeda* production prior to wilderness area establishment (Anon. 1985). We had two disturbance regimes: (1) areas with cut-and-leave suppression and additional wildfire (hereafter designated 'C-L+fire') (*N* = 10), and (2) *P. taeda* stands undisturbed by *D. frontalis* and cut-and-leave but with wildfire (untreated controls, hereafter designated 'fire') (*N* = 9). Fire disturbance was not assessed as a treatment because there were inadequate replications available for each fire regime among the two disturbance events.

Sampling design and assessments:

In each stand, five 0.04-ha (1/10 acre) fixed-radius whole plots were established a minimum of 50 m from the stand edges defined by the USDA Forest Service, and separated by a minimum of 50 m, to survey woody plant vegetation and assess stand characteristics and landscape variables. Ten subplots, five 0.004-ha (1/100 acre) and five 0.0004-ha (1/1000 acre), were nested within each whole plot (0.04-ha) to enhance precision of our vegetation assessments. Whole plots (0.04-ha) were used to assess sawtimber and poletimber (> 12.7 cm DBH), while 0.004-ha subplots were used to assess saplings (≤ 12.7 cm DBH) and large shrubs (≥ 137 cm height), and 0.0004-ha subplots were used to assess seedlings, small shrubs (< 137 cm height), and vines. Thus a surveyed stand contained a total of five 0.04-ha whole plots, 25 0.004-ha subplots, and 25 0.0004-ha subplots. Measurements of vegetation and plot data followed the Common Stand Exam protocols of the USDA Forest Service's Natural Resource Information System (NRIS): Field Sampled Vegetation Module (FSVeg) (Anon. 2003).

In the 0.04-ha whole plots, all living sawtimber- and poletimber-sized trees were used for vegetation assessment. Species identification, tree diameter at breast height (DBH), tree height, and tree crown height (distance to lowest continuous part of the crown) were evaluated. In the 0.004-ha subplots, all live saplings and large shrubs were identified and measured following the same protocol as the whole plots (0.04-ha). Lastly, seedlings, small shrubs, and vines were assessed for species identification

and plant height in each of the 0.0004-ha subplots.

Elevation, aspect, slope (%), and slope position (slope summit, slope shoulder, backslope, footslope, toeslope, and valley bottom) were assessed in each whole plot (Anon. 2003). Tree growth over the past ten years was estimated by increment boring two dominant hardwoods of the same species and two dominant *Pinus* spp. in each whole plot (0.04-ha), and measuring the width of each of the last ten growth rings to the nearest 0.13 cm (1/20 inch). Ground surface cover (%) was visually estimated within the whole plots (0.04-ha) using the following classification: trees, shrubs, forbs, grasses, leaf litter, and coarse woody debris (> 6 cm diameter) (Anon. 2003). In addition, forest stand age and disturbance history (wildfire) were assessed for each stand using historic data (Anon. 1985).

Forest modeling

Forest structure and forest type (Donnelly et al. 2001) were modeled 50 years into the future from 2004 or 2005 utilizing the southern variant of the Forest Vegetation Simulator (FVS) (Anon. 2001). FVS is an individual-tree, nonspatial forest growth model built from the core model Prognosis (Stage 1973). FVS is nationally supported, and highly adaptable to regions throughout the U.S. (Robinson & Monserud 2003). FVS is adequate for simulating long-term processes where growth is the main component (Teck et al. 1996).

FVS accounts for four factors to predict vegetation composition: large-tree model, small-tree model, establishment model, and mortality model (Donnelly et al. 2001). The large-tree model accounts for three factors of individual tree characteristics (current DBH, height, crown ratio), aggregate attributes of tree neighbors (basal area per acre, basal area of large diameter trees), and the site environment surrounding trees (site forest type and site's relative geographic location in the variant). Small-tree (7.5-12.7 cm DBH) heights are bounded with large-tree height growth estimates over an overlapping diameter range to assure a smooth transition in height growth estimates to the large-tree model. The establishment model introduces two sources of regeneration in the FVS, seedlings and stump sprouts.

Two types of mortality, background and density related, are used for the mortality model. Background mortality accounts for occasional mortality in stands when stand density is below a specified level. Density related mortality determines mortality rates for individual trees, based on the relationship between stand density and maximum stand density specified by the default or input.

Assessed tree data and landscape variables, including species, DBH, height, height to crown, radial growth, and ecological region, were incorporated into FVS to

calibrate and model forest stand succession on a five year cycle (Donnelly et al. 2001). *P. taeda* stand parameters (maximum stand density index and maximum basal area) were used to regulate forest stand modeling. Predicted forest type and stand characteristics were obtained from FVS by using the main output, and stand and stocking simulators.

The southern variant of FVS is a relatively recent development, and verification of its accuracy is lacking. Consequently our modeling results should be interpreted with caution. However, other FVS variants built from the same core are accurate for predicted tree density and diameter, and stand characteristics are within ± 20% of measured data (Fule et al. 2004). FVS variants typically under-predict top height and basal area, but model predictions are consistent with the distribution of diameter size classes (Lacerte et al. 2004). Long-term modeling may pose problems for FVS (Groot et al. 2004), but we make fairly short-term projections (50 years) that should not significantly exaggerate stand characteristics.

Statistical analysis

Plant species abundance, richness, diversity, and evenness were assessed for the woody plant community between the two disturbance regimes (C-L+fire and fire). Diversity and evenness were calculated as follows (Magurran 1988):

Diversity: Shannon index $H' = -\sum p_i \ln p_i$;

Evenness: Pielou's evenness index $J' = H' (\ln S)^{-1}$; where p_i is the proportion of species i and S is species richness. Plant indices were calculated for three size classes: (1) sawtimber and poletimber, (2) saplings and large shrubs, and (3) seedlings, small shrubs, and vines. Plant counts from the sapling and large shrub and the seedling, small shrub, and vine size classes were adjusted to 0.04-ha size whole plots to standardize counts for all analyses.

Forest stand characteristics, including tree diameter and height, tree basal area, and total tree volume, were calculated for two size classes (sawtimber and poletimber and saplings and large shrubs). Total volume was calculated using total tree height, whereas sawlog volume was calculated using tree crown height for trees ≥ 25 cm DBH.

Our stand characteristics for forest modeling focused on sawtimber (≥ 25.4 cm DBH), poletimber (12.7-25.3 cm DBH), and saplings (0.1-12.6 cm DBH). In each category we assessed predicted tree height, tree density, basal area, and total tree volume by FVS for all tree species, and specifically for *P. taeda*. Stand characteristics were also described using sawlog volume for all species and for *P. taeda* in the sawtimber size class.

We used a mixed-model analysis of variance with a completely randomized design (PROC MIXED, SAS 1997) to test for differences in community parameters, forest stand characteristics, ground cover, and modeled forest data between the two disturbance regimes. Disturbance regimes were used as the fixed effect, with *P. taeda* stands as random effects. Whole and subplots were used as subsamples. Data were transformed if they did not meet underlying assumptions of normality and homogeneity of variances (Levene's equal variances test) for analyses of variance. All data are presented as untransformed means (s.e.) to assist with interpretation. For all analyses, treatment effects were considered statistically significant if $P \le 0.05$. Additional attention was given to those effects of marginal significance ($P = 0.09$-0.05) due to the complexity and variability of the system.

We used a multivariate analysis of variance (MANOVA) to assess differences in the five most abundant plant species for each size class (PROC GLM, SAS; Anon. 1997), using Wilk's λ to test for overall significance in the MANOVA. The same statistical design, effects, and assumption tests were used for this analysis as the ANOVA.

Patterns of species assemblages with environmental variables (aspect, elevation, slope, slope position, stand age, fire, and stand treatment) were assessed using canonical correspondence analysis (CCA) and presented graphically as a biplot (Gabriel 1981; ter Braak 1986; PC-ORD, McCune & Mefford 1999). Intraset correlations (≥ ±0.60) are used to show the relative importance of each environmental variable in the overall community (ter Braak 1986). Eigenvalues are presented to show variance extracted by environmental variables.

Monte Carlo permutations (300 randomizations) were used to test if relationships between environmental variables and species data were attributed to random events (PC-ORD, McCune & Mefford 1999). Because all variables were significant ($P < 0.05$) both individually and collectively when they were incorporated into the CCA, all were kept in the analysis.

Measured environmental variables describe individual whole plot (0.04-ha) conditions due to variability within each stand, and do not sufficiently correspond to the entire stand. As a result, environmental variables and plant species counts were incorporated into the CCA at the whole plot level (0.04-ha, $N = 95$) and not at the stand level. Densities of individual species in the subplots were adjusted to the whole plot size, and all plots and all species were used in the analysis. Aspect was transformed to a 0-16 scale, from 0 = NNE 40° (most mesic) to 16 = SSW 220° (most xeric), modified from Dargie (1984). Slope (%), elevation, and stand age at the time of cut-and-leave disturbance were integrated as separate integers. Plot elevation ranged from about 5 to 90 m, and stand ages span from 44-81 years, with an average age of 52 years for C-L+fire stands and 54 years

Table 1. Effects of cut-and-leave suppression with subsequent wildfire (C-L+fire) on the density of the five most abundant woody plant species (ha) in *Pinus taeda* stands in Kisatchie Hills Wilderness.

Species	Disturbance effect±	Disturbance regime[†]	
		C-L+fire (ha^{-1})	Fire (ha^{-1})
A. Sawtimber and poletimber (≥12.7 cm DBH)			
MANOVA	$1.22_{5, 13}$/ n.s.		
1. *Pinus taeda*	$0.41_{1, 17}$/ n.s.	150 (16.2)	129 (16.6)
2. *Pinus palustris*	$6.11_{1, 17}$/ **	10 (3.9)	50.6 (9.65)
3. *Quercus falcata*	$0.02_{1, 17}$/ n.s.	19 (4.6)	17.8 (6.89)
4. *Liquidambar styraciflua*	$0.76_{1, 17}$/ n.s.	16.5 (3.47)	11.1 (3.69)
5. *Quercus alba*	$0.05_{1, 17}$/ n.s.	11.5 (3.79)	10 (3.8)
B. Saplings and large shrubs (≥137 cm height)			
MANOVA	$2.89_{5, 13}$/ n.s.		
1. *Ilex vomitoria*	$9.55_{1, 17}$/ ***	2 515 (489)	6 822 (1 272)
2. *Pinus taeda*	$0.72_{1, 17}$/ n.s.	4 715 (820)	850 (442)
3. *Vaccinium elliottii*	$0.07_{1, 17}$/ n.s.	2 935 (715)	2 216 (832)
4. *Acer rubrum*	$0.03_{1, 17}$/ n.s.	1 400 (277)	1 583 (426)
5. *Liquidambar styraciflua*	$0.69_{1, 17}$/ n.s.	1 165 (208)	1 022 (230)
C. Seedlings, small shrubs (<137 cm height) and vines			
MANOVA	$2.25_{5, 13}$/ n.s.		
1. *Gelsemium sempervirens*	$1.17_{1, 17}$/ n.s.	57 055 (10 743)	90 222 (13 496)
2. *Ilex vomitoria*	$9.55_{1, 17}$/ ***	24 150 (3 999)	110 944 (19 028)
3. *Smilax glauca*	$0.01_{1, 17}$/ n.s.	40 700 (11 322)	41 900 (8 487)
4. *Vaccinium elliottii*	$0.07_{1, 17}$/ n.s.	31 650 (5 595)	35 000 (7 346)
5. *Pinus taeda*	$0.72_{1, 17}$/ n.s.	18 200 (5 975)	38 277 (10 143)

[†]Means (SE) from mixed-model analysis: ±F_{df} / P-value (n.s.= $P ≥ 0.1$; * = $P < 0.1$; ** = $P ≤ 0.05$; *** = $P ≤ 0.01$; **** = $P ≤ 0.0001$).

for fire stands. Slope position was modified by ranking positions 1-6, from low (1 = valley bottom) to high (6 = slope summit) (Kavanagh and Stanton 2005). The four events of wildfire disturbance were ranked based on the intensity and frequency of disturbance, with the two low-intensity 2000 fires ranked equally as the least intense, followed by the high-intensity 1987 fire, and the interaction of the low- and high-intensity fires as the most intense. Disturbance regimes (C-L and undisturbed pine stands+fire) were incorporated into the analysis as dummy variables (K-1) (Blake & Schuette 2000).

Finally, forest types predicted by the FVS were analyzed using a χ^2 analysis with Fischer's exact test. χ^2 analysis tested the frequency of predicted *Pinus* spp.-dominated (*Pinus* spp. basal area > 50% of the dominant canopy species) or hardwood-dominated (hardwood basal area > 50% of the dominant canopy species) forest types across treatments, and the occurrence of predicted *Pinus* spp.-dominated canopies to predicted hardwood-dominated canopies between the two treatments.

Results

In Kisatchie Hills, 24 091 individual woody plants representing 85 species in 33 families were assessed over the two year period (App. 1). A total of 12 677 individuals were assessed in C-L+fire stands, whereas 11 414 individuals were assessed in fire stands. Only statistically significant differences are addressed.

Sawtimber and poletimber

P. taeda, *P. palustris*, *Quercus falcata*, *Liquidambar styraciflua*, and *Acer rubrum*, dominated the overstory and midstory (Table 1A). The MANOVA revealed no differences between the two disturbance regimes. However, the abundance of *P. palustris* significantly decreased 80% following the C-L+fire disturbance (Table 1A).

Trees in fire stands had significantly greater diameter (35%) relative to C-L+fire stands (Table 2A). C-L+fire significantly reduced sawtimber and poletimber basal area by 60%, total volume by 77%, and sawlog volume by 85% compared to fire stands (Table 2A).

In the predicted sawtimber size class (≥ 25.4 cm DBH), height decreased 22% following C-L+fire relative to fire stands (Table 3A). Predicted sawlog volume decreased 44% after C-L+fire compared to fire stands, but this difference was only marginally significant (P = 0.06, Table 3A). Not surprisingly, the predicted height of *P. taeda* sawtimber decreased significantly by 25% in C-L+fire stands compared to fire stands (Table 3A).

Predicted basal area and total volume of poletimber increased 272% and 236%, respectively, following C-L+fire compared to fire stands, but these increases were of marginal significance (P = 0.09, Table 3B). C-L+fire stands had significantly greater predicted density (300%), basal area (420%), and total volume (380%) of *P. taeda* poletimber relative to stands with fire alone (Table 3B).

Table 2. Stand characteristics following cut-and-leave suppression with additional wildfire (C-L+fire) in *Pinus taeda* stands in Kisatchie Hills Wilderness.

Parameter	Disturbance effect$^{\pm}$	Disturbance regime† C-L+fire	Fire
A. sawtimber and poletimber (≥ 12.7 cm DBH)			
diameter (cm)	$56.7_{1,16}$/ ****	19 (0.45)	30 (0.78)
height (m)	$0.88_{1,16}$/ n.s.	17 (4.63)	21 (0.77)
basal area (m².ha⁻¹)	$20.5_{1,16}$/ ***	9.72 (0.95)	24.5 (2.27)
total volume (m³.ha⁻¹)	$15.9_{1,16}$/ ***	50 (6.8)	216 (24)
sawlog volume (m³.ha⁻¹)	$8.96_{1,16}$/ ***	17 (4.73)	112 (15.2)
B. saplings and large shrubs (≥ 137 cm height)			
diameter (cm)	$11.4_{1,16}$/ ***	3.69 (0.21)	2.02 (0.19)
height (m)	$3.40_{1,16}$/ *	4.44 (0.24)	3.14 (0.31)
basal area (m².ha⁻¹)	$21.3_{1,16}$/ ***	7.35 (0.59)	1.96 (0.47)
total volume (m³.ha⁻¹)	$20.8_{1,16}$/ ***	93 (9.26)	21 (4.92)
C. ground cover (%)			
tree	$0.04_{1,16}$/ n.s.	14 (1.60)	14 (1.52)
shrub	$3.21_{1,16}$/ *	19 (1.92)	24 (2.68)
forb	$0.01_{1,16}$/ n.s	5.67 (1.10)	4.84 (1.82)
grass	$0.38_{1,16}$/ n.s.	16 (3.01)	20 (3.91)
wood	$10.3_{1,16}$/ ***	4.27 (0.45)	1.51 (0.48)
litter	$0.14_{1,16}$/ n.s.	34 (0.57)	33 (0.04)

†Means (SE) from mixed-model analysis: $^{\pm}F_{df}$ / P-value (n.s.= $P \geq 0.1$; * = $P < 0.1$; ** = $P \leq 0.05$; *** = $P \leq 0.01$; **** = $P \leq 0.0001$).

Table 3. Predicted stand characteristics (50 yr) after cut-and-leave suppression with subsequent wildfire (C-L+fire) in central Louisiana.

Parameter	Disturbance effect$^{\pm}$	Disturbance regime† C-L+fire	Fire
A. modeled sawtimber (≥ 25.4 cm DBH)			
height (m)	$9.13_{1,16}$/ ***	17 (1.06)	22 (1.71)
density (ha⁻¹)	$1.77_{1,16}$/ n.s.	251 (49)	173 (30)
basal area (m².ha⁻¹)	$0.01_{1,16}$/ n.s.	17 (2.83)	17 (3.44)
total volume (m³.ha⁻¹)	$1.92_{1,16}$/ n.s.	92 (17)	133 (25)
sawlog volume (m³.ha⁻¹)	$3.93_{1,16}$/ n.s.	59 (13)	106 (22)
P. taeda height (m)	$12.1_{1,16}$/ ***	14 (1.56)	23 (2.21)
P. taeda density (ha⁻¹)	$2.89_{1,16}$/ n.s.	147 (28)	82 (25)
P. taeda basal area (m².ha⁻¹)	$0.03_{1,16}$/ n.s.	10.4 (2.72)	9.44 (3.46)
total *P. taeda* volume (m³.ha⁻¹)	$0.44_{1,16}$/ n.s.	55 (14)	71 (20)
total *P. taeda* sawlog volume (m³.ha⁻¹)	$1.31_{1,16}$/ n.s.	40 (14)	65 (20)
B. Modeled poletimber (≥ 12.7 cm DBH)			
height (m)	$1.07_{1,16}$/ n.s.	11 (1.45)	13 (0.36)
density (ha⁻¹)	$2.74_{1,16}$/ n.s.	956 (397)	265 (69)
basal area (m².ha⁻¹)	$3.27_{1,16}$/ *	19.6 (7.60)	5.28 (1.22)
total volume (m³.ha⁻¹)	$3.16_{1,16}$/ *	92 (35)	27 (6.4)
P. taeda height (m)	$0.63_{1,16}$/ n.s.	12 (1.88)	10 (1.38)
P. taeda tree density (ha⁻¹)	$4.97_{1,16}$/ **	558 (169)	139 (61)
P. taeda basal area (m².ha⁻¹)	$8.53_{1,16}$***	11 (2.87)	2.2 (0.89)
total *P. taeda* volume (m³.ha⁻¹)	$8.51_{1,16}$/ ***	54 (13)	11 (4.7)
C. Modeled saplings (> 137 cm)			
height (m)	$1.40_{1,16}$/ n.s.	8.49 (0.42)	9.19 (0.54)
density (ha⁻¹)	$1.08_{1,16}$/ n.s.	10 234 (6 164)	3 614 (855)
basal area (m².ha⁻¹)	$0.65_{1,16}$/ n.s.	23 (3.19)	20 (4.33)
total volume (m³.ha⁻¹)	$2.29_{1,16}$/ n.s.	54 (13)	30 (8.2)
P. taeda height (m)	$0.81_{1,16}$/ n.s.	11.0 (0.77)	8.75 (2.53)
P. taeda density (ha⁻¹)	$0.27_{1,16}$/ n.s.	697 (283)	508 (226)
P. taeda basal area (m².ha⁻¹)	$0.02_{1,16}$/ n.s.	4.97 (2.13)	4.55 (2.07)
total *P. taeda* volume (m³.ha⁻¹)	$0.12_{1,16}$/ n.s.	27 (13)	21 (9.3)

†Means (SE) from mixed-model analysis: $^{\pm}F_{df}$ / P-value (n.s.= $P \geq 0.1$; * = $P < 0.1$; ** = $P \leq 0.05$; *** = $P \leq 0.01$; **** = $P \leq 0.0001$).

Table 4. Influence of cut-and-leave suppression with subsequent wildfire (C-L+fire) on the woody plant community (ha) in *Pinus taeda* stands in Kisatchie Hills Wilderness.

Parameter	Disturbance effect[±]	Disturbance regime[†]	
		C-L+fire (ha^{-1})	Fire (ha^{-1})
A. Sawtimber and poletimber (≥ 12.7 cm DBH)			
Abundance	$0.04_{1, 16}$ / n.s.	275 (21.4)	282 (25.3)
Richness	$0.01_{1, 16}$ / n.s.	3.66 (0.32)	3.67 (0.33)
Diversity	$0.06_{1, 16}$ / n.s.	0.87 (0.09)	0.92 (0.08)
Evenness	$1.51_{1, 16}$ / n.s.	0.629 (0.05)	0.734 (0.04)
B. Saplings and large shrubs (≥ 137 cm height)			
Abundance	$1.48_{1, 16}$ / n.s.	22 540 (1 933)	16 444 (2 757)
Richness	$10.4_{1, 16}$ / ***	12 (0.84)	7.4 (0.68)
Diversity	$2.46_{1, 16}$ / n.s.	1.77 (0.94)	1.34 (0.90)
Evenness	$0.04_{1, 16}$ / n.s.	0.721 (0.03)	0.709 (0.03)
C. seedlings, small shrubs (< 137 cm height), and vines			
Abundance	$3.06_{1, 16}$ / n.s.	369 345 (24 900)	479 405 (36 475)
Richness	$2.03_{1, 16}$ / n.s.	16 (0.71)	14 (0.73)
Diversity	$5.13_{1, 16}$ / **	2.10 (0.06)	1.84 (0.06)
Evenness	$4.40_{1, 16}$ / **	0.771 (0.01)	0.722 (0.10)

[†]Means (SE) from mixed-model analysis: [±]F_{df} / P-value (n.s.= $P \geq 0.1$; * = $P < 0.1$; ** = $P \leq 0.05$; *** = $P \leq 0.01$; **** = $P \leq 0.0001$).

Saplings and large shrubs (≥ 137 cm height)

C-L+fire significantly increased sapling and large shrub richness 61% relative to fire stands (Table 4B). *Ilex vomitoria*, *P. taeda*, *Vaccinium elliottii*, *A. rubrum* and *L. styraciflua* represent the most abundant woody species in the understory (Table 1B). C-L+fire significantly decreased 63% the abundance of *I. vomitoria* (Table 1B).

Diameter of saplings and large shrubs increased significantly 83% in C-L+fire stands relative to fire stands (Table 2B). Marginally significant differences were evident for height between disturbance regimes ($P = 0.08$, Table 2B); C-L+fire increased height 41% relative to fire stands. Basal area increased significantly 74% and tree volume 77% following C-L+fire relative to fire stands (Table 2B).

Seedlings, small shrubs (< 137 cm height), and vines

In the seedling, small shrub, and vine size class, the diversity and evenness of seedlings, small shrubs, and vines significantly increased 14% and 7%, respectively, in C-L+fire relative to fire stands (Table 4C). *Gelsemium sempervirens*, *I. vomitoria*, *Smilax glauca*, *V. elliottii*, and *P. taeda* were the most abundant of this size class (Table 1C). Abundance of *I. vomitoria* significantly decreased 37% following C-L+fire disturbance (Table 1C). In C-L+fire stands, shrub ground cover decreased marginally 22% ($P = 0.09$) and coarse woody debris increased significantly 64% relative to fire stands (Table 2C).

Plant community

Plots receiving either of the two disturbances, C-L+fire and fire, did not sufficiently account for variance in the CCA. However, slope position and elevation explained the greatest variance along the first ordination axis (Fig. 1). Species associated with higher slope positions (slope summit and shoulder) and elevations included *G. sempervirens*, several *Vaccinium* spp., *P. taeda*, and *I. vomitoria*, and are depicted to the right along Axis 1 (Fig. 1). *Fagus grandifolia*, *Q. nigra*, *Magnolia grandiflora*, and *Carya cordiformis*, were related to lower slope positions (valley bottom and toe slope) and elevations, and presented to the left along Axis 1 (Fig. 1). The canonical correspondence analysis (CCA) accounted for 15.0% of the variation in the data along the first three axes (Fig. 1). Axis 1 accounted for 7.6% of the variability, with an eigenvalue of 0.33. Intraset correlation coefficients for slope position and elevation along Axis 1 are 0.78 and 0.65, respectively

Fire intensity and frequency explained variance along Axis 2, with *P. taeda*, *Q. falcata*, *Crataegus marshallii,* and, *P. palustris* associated with the low-intensity 2000 fires, and plotted to the bottom along Axis 2 (Fig. 1). *I. vomitoria*, *Rubus trivialis*, *Morella cerifera*, and *Q. incana*, were associated with plots receiving the two fire events, and plotted to the top along Axis 2 (Fig. 1). Axis 2 accounted for 4.4% of the variability, with an eigenvalue of 0.19 (Fig. 1). The intraset correlation coefficient for fire intensity along Axis 2 is 0.90.
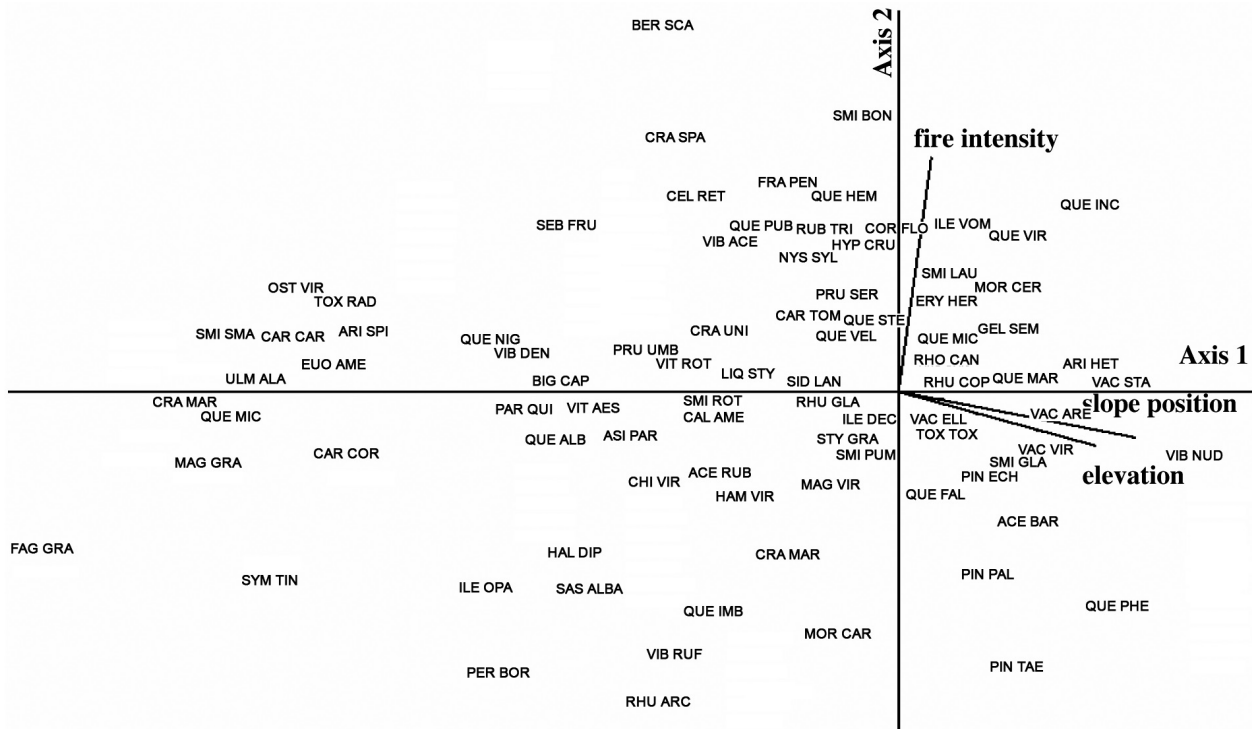
Fig. 1. First and second ordination axes from canonical correspondence analysis depicting relationships between environmental variables and woody species composition following cut-and-leave suppression with subsequent wildfire, and in *P. taeda* stands with wildfire. Slope position and elevation explain variance along Axis 1, with fire intensity explaining variance along Axis 2. Higher slope position is plotted to the right along Axis 1, whereas lower slope position is plotted to the left. Fire intensity explains variance along Axis 2, with higher fire intensity at the top and lower fire intensity plotted to the bottom. Species names (App. 1) are the first three letters of the genus and species.

Stand age was associated with the third ordination axis. *A. rubrum, Nyssa sylvatica, P. taeda,* and *I. vomitoria* were associated with younger stands, and were depicted to the bottom along Axis 3 (Fig. 2), whereas *F. grandifolia, Q. stellata, Q. falcata,* and *C. cordiformis* were associated with older stands, and presented at the top (Fig. 2). Axis 3 accounted for 3.1% of the variability and represented an eigenvalue of 0.14 (Fig. 2). The intraset correlation coefficient for stand age along Axis 3 is 0.77.

Forest type

Using FVS, four distinct forest types were predicted across C-L+fire and fire stands: *P. taeda* (47%), *P. taeda/* hardwood (32%), mixed upland hardwood (16%), and *P. palustris/ Quercus* spp. (5%). C-L+fire stands were predicted to sustain *P. taeda* composition 50% of the time, to develop into *P. taeda/* hardwood (30%), or to transition to mixed upland hardwood (20%). Fire stands were predicted to maintain *P. taeda* composition 45% of the time, to develop into *P. taeda/* hardwood (33%), or to transition

to mixed upland hardwood (11%) or *P. palustris/ Quercus* spp. (11%). *Pinus* spp.-dominated stands occurred more frequently than hardwood-dominated stands (84% vs. 16%) across the two disturbance regimes ($\chi^2_{df=1}$ = 9.8, P = 0.002). Predicted forest types did not differ between the two regimes ($\chi^2_{df=1}$ = 0.19, P = 0.4). C-L+fire stands were predicted to sustain *Pinus* spp. dominance 80% of the time, and transition to hardwood dominance 20% of the time. Fire stands maintained *Pinus* spp. dominance 89% of the time and shifted to hardwood-dominated forests 11% of the time.
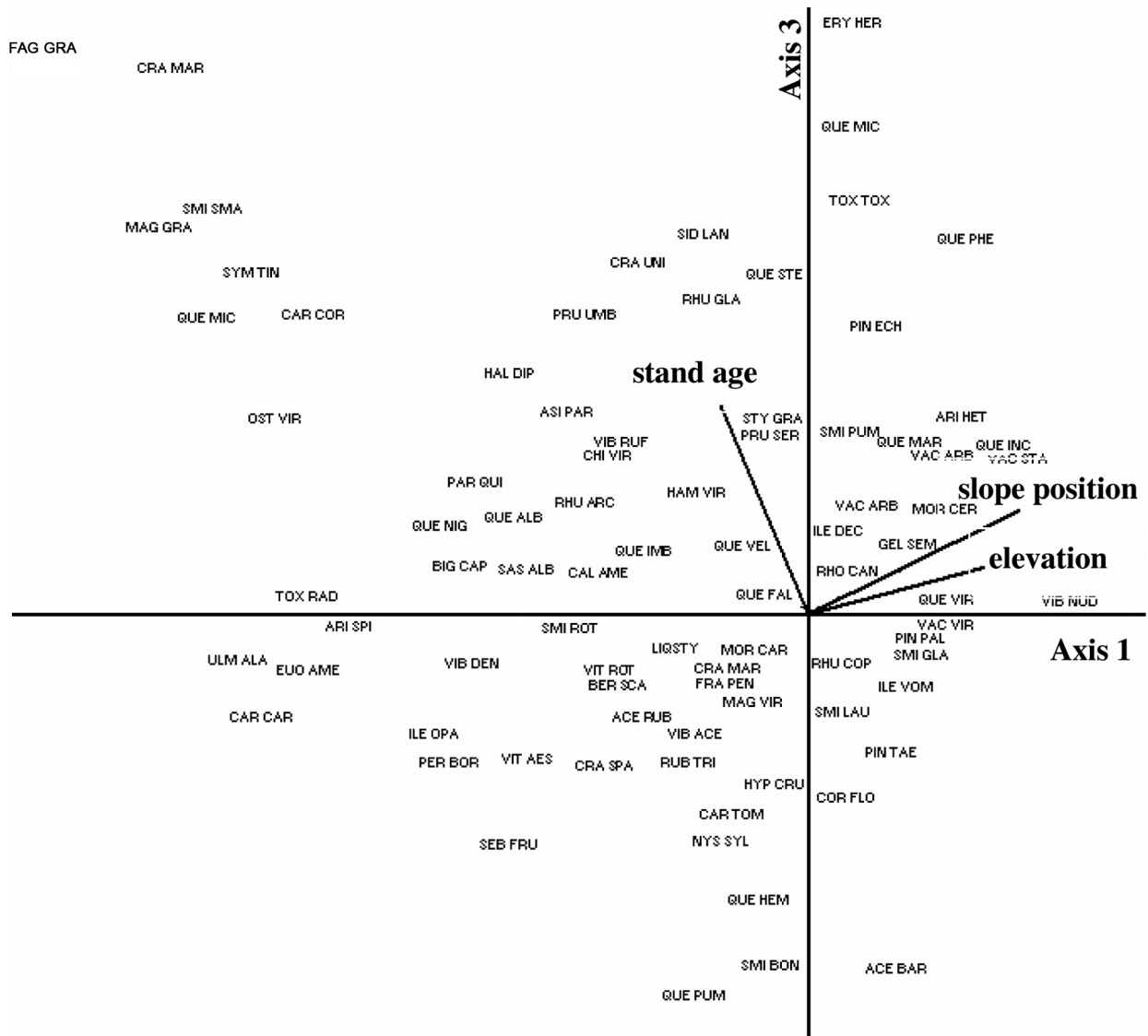
Fig. 2. First and third ordination axes from canonical correspondence analysis depicting relationships between environmental variables and woody species composition following cut-and-leave suppression with subsequent wildfire, and in *Pinus taeda* stands with wildfire. Variance along Axis 1 is explained by slope position and elevation. Variance along Axis 3 is related to stand age. Older forest stands are plotted toward the top of the ordination, whereas younger forest stands are plotted to the bottom of Axis 3. Species names (App. 1) are the first three letters of the scientific name.

Discussion

D. frontalis, wildfire, and cut-and-leave suppression are intermittent and recurring disturbances influencing vegetation succession on the Western Gulf Coastal Plain. Tree mortality from C-L+fire considerably lowered saw-timber and poletimber height, basal area, total volume, and sawlog volume relative to the corresponding 40-80 years old fire-only *P. taeda* stands. The 20 years following overstory mortality from cut-and-leave suppression, recruitment primarily of *P. taeda* into the sawtimber and

poletimber size classes eliminated the differences in the plant community, except for *P. palustris* which showed little natural regeneration. However, evidence of major overstory mortality is still visible in the understory. C-L+fire stands contain greater sapling and large shrub richness, consisting primarily of shade-intolerant species (*I. vomitoria*, *P. taeda*, *V. elliottii* and *L. styraciflua*), perhaps from microclimate changes and release from competition associated with canopy loss (Phillips & Shure 1990). Additional wildfire disturbance may have limited understory density by thinning the abundant *I. vomitoria*,

and shade-tolerant, late-successional species.

Predictably, saplings and shrubs responded to the canopy loss in C-L stands with greater gains in diameter, height, basal area, and volume (Lugo & Scatena 1996). However, dense growth from saplings and large shrubs appears to be limiting the abundance and richness of seedlings, small shrubs, and vines on the forest floor, although their diversity and evenness increased, probably due to initial increases in shade-intolerant vegetation, which are still present. Harrington et al. (2000) found tree species diversity in *Pinus*/hardwood stands subjected only to *D. frontalis*-caused mortality surpassed undisturbed stands, because hardwood abundance increased following *Pinus* mortality.

Ordination analysis demonstrates that cut-and-leave suppression is not the primary gradient explaining variance among vegetation assemblages, and does not appear to alter forest succession differently than areas only with wildfire. Rather, the ordination is more strongly influenced by initial forest composition, and appears to be driven by gradients inherent to the landscape (Halpern 1988). *Pinus* spp. regeneration is more dominant in upper slope positions whereas hardwoods are more plentiful in lower, more mesic positions. Ordination techniques also supported separation of *P. taeda* forests along a moisture gradient in the piedmont of Alabama (Golden 1979).

Fire intensity and frequency explained vegetation assemblages along the second ordination axis. Because these wildfires occurred within wilderness boundaries, limited information on fire characteristics are available; fire intensity and speed of spread are unknown. As a result, fire frequency and intensity classifications are not direct measures and represent general groupings that were defined by fuel load from pine mortality and fire occurrence. C-L+fire stands mostly received the 1987 high-intensity fire and the 2000 low-intensity fire. Plots receiving frequent surface fires (1987 and 2000) primarily represent stands without cut-and-leave suppression. Frequent surface fires (1987 and 2000) favored shrub, vine, and scrub oak species common to early-successional communities (Burns & Honkala 1990b; Gleason & Cronquist 1991). Similar vegetation occurred in plots receiving only the 1987 high-intensity fire. Regardless of stand treatments, vegetation assemblages were comparable among plots that received different fire regimes. However, the low-intensity 2000 fires that dominated the C-L+fire treatment were associated mainly with trees, probably only impacting small shrubs and vegetation on the forest floor. In both northern and central hardwood forests, low-intensity fires did not impact overstory trees but did substantially alter understory composition and density (Reich et al. 1990; Coleman & Rieske 2006).

Stand age at the time of cut-and-leave suppression explained the final CCA gradient. Species associated with younger stands appear to maintain *Pinus* composition

and represent a mix of both shade-tolerant and intolerant vegetation (Burns & Honkala 1990a, b). In contrast, species in older stands were associated with shade-tolerant and climax community species. In an East Texas forest, *F. grandifolia* and *M. grandiflora* obtained canopy dominance following selective logging of *Pinus* spp., similar to cut-and-leave suppression (Glitzenstein et al. 1986).

P. taeda regeneration was predicted to advance to the midstory and attain canopy dominance or co-dominance following each disturbance regime in FVS simulations although dominant, seed-bearing *P. taeda* were cut for beetle suppression. *Pinus* spp. were also expected to return to the canopy in gaps along the Eastern Gulf Coastal Plain and Piedmont of the southeastern U.S. following *D. frontalis*-caused mortality because of closer seed sources, reduced competition, and initially high *Pinus* spp. densities (Skeen 1976; Rantis & Johnson 2002). In contrast, small-scale mortality from *D. frontalis* shifted canopy dominance from dominant or co-dominant *Pinus* spp. forests to primarily hardwood forest types in southeastern forests (Balch 1928; Shelton & Cain 1999; Duncan & Linhoss 2005). Lack of *Pinus* spp. regeneration was attributed to inadequate exposed soil and competition from trees along gap edges or taller hardwoods, which was not seen in our study due to the occurrence of fire and monoculture canopies dominated by *P. taeda*.

Interacting disturbances from cut-and-leave suppression and wildfire are predicted to continue the cycle of mortality from *D. frontalis* by promoting *P. taeda*. Seventy year old C-L+fire stands have a predicted *P. taeda* basal area for sawtimber and poletimber ($21 \text{ m}^2.\text{ha}^{-1}$) that is of high hazard for future *D. frontalis* outbreaks. In fire stands, predicted *P. taeda* basal area represents a low hazard ($11 \text{ m}^2.\text{ha}^{-1}$) for future *D. frontalis* (Mason et al. 1985). Hardwood basal area of sawtimber- and poletimber-size represents $\geq 40\%$ of the total basal area in both disturbance regimes (Table 4), which can enhance stress to *Pinus* spp. by increasing competition for nutrients and light, therefore escalating susceptibility to *D. frontalis*-caused mortality (Lorio 1980). However, additional hardwood basal area could reduce the hazard of *D. frontalis* outbreaks by interfering beetle pheromones and increasing non-host volatiles.

Losses solely of prominent overstory *Pinus* spp. can accelerate succession towards hardwoods or climax communities, instead of promoting early-successional *Pinus* spp. communities. However, our study demonstrates that cut-and-leave suppression with additional wildfire disturbance maintains *Pinus* spp. composition, and also maintains the forest's susceptibility to future *D. frontalis* outbreaks. Initial composition, landscape position, forest stand age, and subsequent disturbances also appear to play a role in future forest composition, especially following cut-and-leave suppression.

References

Anon. 1985. *Continuous Inventory Stand Conditions (CISC) data*. Kisatchie National Forest, Kisatchie Hills Wilderness Area. USDA Forest Service, Natchitoches, LA, US.

Anon. 1987. *Final environment impact statement for the suppression of the southern pine beetle*. Southern Region. Volume 1. USDA Forest Service, Region 8, Management Bulletin R8-MB-2. Asheville, NC, US.

Anon. 1990. *Soil survey of Natchitoches parish, Louisiana*. USDA Soil Conservation Service, Forest, Service, Louisiana Agricultural Experimental Station, Louisiana Soil and Water Conservation Committee. Natchitoches, LA, US.

Anon. 1997. *SAS/STAT software: changes and enhancements through release 6.12*. SAS Institute, Cary, NC, US.

Anon. 2001. *Forest Vegetation Simulator (FVS), Southern variant*. USDA Forest Service, Rocky Mountain Research Station. Fort Collins, CO, US.

Anon. 2003. *Natural resource information service (NRIS): Field sampled vegetation (FSVeg) Common Stand Exam*. V1.5.1. USDA Forest Service, Rocky Mountain Research Station. Fort Collins, CO, US.

Anon. 2005. *The PLANTS Database, Version 3.5*. Data compiled from various sources by Mark W. Skinner. National Plant Data Center, Baton Rouge, LA, US. http://www.plants.usda.gov.

Anon. 2007. (National Weather Service, southern region headquarters) 2001. http://www.srh.weather.gov/ shv/coop_climate/Natchitoches_LA. [accessed 16 May 2007].

Addor, M.L. & Birkhoff, J. 2004. *Bankhead National Forest health and restoration initiative: final report*. National Resources Leadership Institute, Raleigh, NC, US.

Baker, J.B. & Langdon, O.G. 1990. *Pinus taeda* L. Loblolly pine. In: Burns, R.M. & Honkala, B.H. (eds.) *Silvics of North America, Vol. 1. Conifers*, pp. 497-512. USDA Forest Service Agricultural Handbook 654. Washington, DC, US.

Balch, R.E. 1928. *The influence of the southern pine beetle on forest composition in western North Carolina*. M.Sc. Thesis, New York State College of Forestry, Syracuse, NY, US.

Billings, R.F. 1980. Direct Control. In: Thatcher, R.C., Searcy, J.L., Coster, J.E. & Hertel, G.D. (eds.) *The southern pine beetle*, pp. 179-194. USDA Forest Service Technical Bulletin 1631, Pineville, LA, US.

Blake, J.G. & Schuette, B. 2000. Restoration of an oak forest in east-central Missouri: Early effects of prescribed burning on woody vegetation. *Forest Ecology and Management* 139: 109-126.

Boyer, W.D. 1990. *Pinus palustris* L. Longleaf pine. In: Burns, R.M. & Honkala, B.H. (eds.) *Silvics of North America, Vol. 1. Conifer*s, pp. 405-412 USDA Forest Service Agricultural Handbook 654. Washington, DC, US.

Burns, R.M. & Honkala, B.H. 1990a. *Silvics of North America, Vol. 1. Conifers*. USDA Forest Service Agricultural Handbook 654. Washington, DC, US.

Burns, R.M. & Honkala, B.H. 1990b. *Silvics of North America, Vol. 2. Hardwoods*. USDA Forest Service Agricultural Handbook 654. Washington, DC, US.

Clarke, S.R. 1995. Impacts of southern pine beetles in special management areas. In: *Proceedings of the 1995 National Silviculture Workshop*, pp. 93-98. Mescalero, NM, May 8-11, 1995. USDA Forest Service General Technical Report RM-GTR-267. Fort Collins, CO, US.

Coleman, T.W. & Rieske, L.K. 2006. Arthropod response to prescription burning at the soil-litter interface in oak-pine forests. *Forest Ecology and Management* 233: 52-60.

Dargie, T.C.D. 1984. On the integrated interpretation of indirect site ordinations: a case study using semi-arid vegetation in south-eastern Spain. *Vegetatio* 55: 37-55.

Donnelly, D., Lilly, B. & Smith, E. 2001. *The southern variant of the Forest Vegetation Simulator*. USDA Forest Service Forest Management Service Center. Fort Collins, CO, US.

Duncan, R.S. & Linhoss, J.E. 2005. Regeneration of virginia pine (*Pinus virginiana*) following southern pine beetle (*Dendroctonus frontalis*) outbreak in the Sipsey Wilderness, Alabama. *Forest Ecology and Management* 212: 65-74.

Fule, P.Z., Crouse, J.E., Cocke, A.E., Moore, M.M. & Covington, W.W. 2004. Changes in canopy fuels and potential fire behavior 1880-2040: Grand Canyon, Arizona. *Ecological Modelling* 175: 231-248.

Gabriel, K.R. 1981. Biplot display of multivariate matrices for inspection of data and diagnosis. In: Barnett, V. (ed.) *Interpreting multivariate data*, pp. 147-173. Wiley, NY, US.

Gleason, H.A. & Cronquist, A. 1991. *Manual of vascular plants of Northeastern United States and adjacent Canada*. 2nd. ed. The New York Botanical Garden, New York, NY, US.

Glitzenstein, J.S., Harcombe, P.A. & Streng, D.R. 1986. Disturbance, succession, and maintenance of species diversity in an east Texas forest. *Ecological Monographs* 56: 243-258.

Golden, M.S. 1979. Forest vegetation of the lower Alabama piedmont. *Ecology* 60: 770-782.

Groot, A., Gauthier, S. & Bergeron, Y. 2004. Stand dynamics modeling approaches for multicohort management of eastern Canadian Boreal Forests. *Silva Fennica* 38: 437-448.

Halpern, C.B. 1988. Early successional pathways and the resistance and resilience of forest communities. *Ecology* 69: 1703-1715.

Harrington, T.B., Xu, M. & Edwards, M.B. 2000. Structural characteristics of late-successional pine-hardwood forest

following recent infestation by southern pine beetle in the Georgia Piedmont, USA. *Natural Areas Journal* 20: 360-365.

Kavanagh, R.P. & Stanton, M.A. 2005. Vertebrate species assemblages and species sensitivity to logging in the forests of north-eastern New South Wales. *Forest Ecology and Management* 209: 309-341.

Lacerte, V., Larocque, G.R., Woods, M., Parton, W.J. & Penner, M. 2004. Testing the Lake States variant of FVS (Forest Vegetation Simulator) for the main forest types of Ontario. *The Forestry Chronicle* 80: 495-506.

Landers, J.L., Van Lear, D.H. & Boyer, W.D. 1995. The longleaf pine forests in the Southeast: requiem or renaissance? *Journal of Forestry* 93: 39-44.

Lorio, Jr., P.L. 1980. Rating stands for susceptibility to SPB. In: Thatcher, R.C., Searcy, J.L., Coster, J.E. & Hertel, G.D. (eds.) *The southern pine beetle*, pp. 153-162. USDA Forest Service Technical Bulletin 1631, Pineville, LA, US.

Lugo, A.E. & Scatena, F.N. 1996. Background and catastrophic tree mortality in tropical moist, wet, and rain forests. *Biotropica* 28: 585-599.

Magurran, A.E. 1988. *Ecological diversity and its measurement*. Princeton University. Princeton, NJ, US.

Mason, G.N., Lorio, P.L., Belanger, R.P. & Nettleton, W.A. 1985. *Rating the susceptibility of stands to southern pine beetle attack*. USDA Forest Service Agricultural Handbook No. 645, Washington, DC, US.

McCune, B. & Mefford, M.J. 1999. PC-ORD. *Multivariate analysis of ecological data, Version 4*. MjM Software Design. Gleneden Beach, OR, US.

Payne, T.L. 1980. Life history and habits. In: Thatcher, R.C., Searcy, J.L., Coster, J.E. & Hertel, G.D. (eds.) *The southern pine beetle*, pp. 7-28. USDA Forest Service Technical Bulletin 1631, Pineville, LA, US.

Phillips, D.L. & Shure, D.J. 1990. Patch-size effects on early succession in southern Appalachian forests. *Ecology* 71: 204-212.

Pickett, S.T.A. & White, P.S. 1985. *The ecology of natural disturbance and patch dynamics*. Academic Press, New York, NY, US.

Quaterman, E. & Keever, C. 1962. Southern mixed hardwood forest: Climax in the southern Coastal Plain, USA. *Ecological Monographs* 32: 167-185.

Rantis, P.A. & Johnson, J.E. 2002. Understory development in canopy gaps of pine and pine-hardwood forests of the upper Coastal Plain of Virginia. *Plant Ecology* 159: 103-115.

Reich, P.B. Abrams, M.D., Ellsworth, D.S., Kruger, E.L. & Tabone, T.J. 1990. Fire affects ecophysiology and community dynamics of central Wisconsin oak forest regeneration. *Ecology* 71: 2179-2190.

Robinson, A.P. & Monserud, R.A. 2003. Criteria for comparing the adaptability of forest growth models. *Forest Ecology and Management* 172: 53-67.

Schowalter, T.D., Coulson, R.N. & Crossley, D.A. 1981. Role of the southern pine beetle and fire in maintenance of structure and function of the southeastern coniferous forest. *Environmental Entomology* 10: 821-825.

Shelton, M.G. & Cain, M.D. 1999. Structure and short-term dynamics of the tree component of a mature pine-oak forest in southeastern Arkansas. *Journal of the Torrey Botanical Society* 126: 32-48.

Skeen, J.N. 1976. Regeneration and survival of woody species in a naturally-created forest opening. *Bulletin of the Torrey Botanical Club* 103: 259-265.

Stage, A.R. 1973. *Prognosis model for stand development*. USDA Forest Service Research Paper INT-137. Intermountain Forest and Range Experiment Station, Ogden, UT, US.

Teck, R.M., Moeur, M. & Eav, B. 1996. Forecasting ecosystems with the Forest Vegetation Simulator. *Journal of Forestry* 94: 7-10.

ter Braak, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167-1179.

Turchin, P., Lorio, P.L., Taylor, A.D. & Billings, R.F. 1999. Why do populations of southern pine beetle (Coleoptera: Scolytidae) fluctuate? *Environmental Entomology* 20: 401-409.

App. 1. Total woody vegetation density surveyed from *Pinus taeda* stands in Kisatchie Hills Wilderness (LA) following cut-and-leave suppression and wildfire (C-L+fire), and *P. taeda* stands with wildfire and no *D. frontalis* associated disturbances (fire). Species names follow USDA, NRCS PLANTS database (Anon. 2005).

			Disturbance regimes	
Species	Abbreviation	Common name	C-L+fire	fire
Family *Aceraceae*				
Acer barbatum	ACEBAR	southern sugar maple	0	6
Acer rubrum	ACERUB	red maple	627	499
Family *Anacardiaceae*				
Rhus aromatica	RHUARO	fragrant sumac	5	0
Rhus glabra	RHUGLA	smooth sumac	1	0
Rhus copallinum var. *latifolia*	RHUCOP	winged sumac	87	44
Toxicodendron radicans	TOXRAD	eastern poison ivy	309	84
Toxicodendron toxicarium	TOXTOX	Atlantic poison oak	12	0
Family *Annonaceae*				
Asimina parviflora	ASIPAR	smallflower pawpaw	7	0
Family *Araliaceae*				
Aralia spinosa	ARISPI	devil's walkingstick	15	1
Family *Aristolochiaceae*				
Aristolochia tomentosa	ARITOM	woolly dutchman's pipe	2	0
Family *Aquifoliaceae*				
Ilex decidua	ILEDEC	possumhaw	22	9
Ilex opaca	ILEOPA	American holly	36	19
Ilex vomitoria	ILEVOM	yaupon	1 240	2 971
Family *Betulaceae*				
Carpinus caroliniana	CARCAR	American hornbeam	82	16
Ostrya virginiana	OSTVIR	hophornbeam	18	30
Family *Bignoniaceae*				
Bignonia capreolata	BIGCAP	crossvine	75	47
Family *Caprifoliaceae*				
Viburnum acerifolium	VIBACE	mapleleaf viburnum	4	12
Viburnum dentatum	VIBDEN	southern arrowwood	23	5
Viburnum nudum	VIBNUD	possumhaw	3	10
Viburnum rufidulum	VIBRUF	rusty blackhaw	8	0
Family *Celastraceae*				
Euonymus americana	EUOAME	strawberry bush	10	0
Family *Cornaceae*				
Cornus florida	CORFLO	flowering dogwood	18	45
Family *Ericaceae*				
Rhododendron canescens	RHOCAN	sweet mountain azalea	41	16
Vaccinium arboreum	VACARB	farkleberry	470	428
Vaccinium elliottii	VACELL	Elliott's blueberry	1 220	1 029
Vaccinium stamineum	VACSTA	deerberry	44	134
Vaccinium virgatum	VACVIR	small flower blueberry	468	461
Family *Euphorbiaceae*				
Sebastiania fruticosa	SEBFRU	Gulf Sebastian-bush	26	30
Family *Fagaceae*				
Fagus grandifolia	FAGGRA	American beech	18	43
Erythrina herbacea	ERYHER	redcardinal	6	0
Quercus falcata	QUEFAL	southern red oak	172	121
Quercus hemisphaerica				
var. *hemisphaerica*	QUEHEM	Darlington oak	0	5
Quercus imbricaria	QUEIMB	shingle oak	2	0
Quercus incana	QUEINC	bluejack oak	14	42
Quercus marilandica	QUEMAR	blackjack oak	157	35
Quercus michauxii	QUEMIC	swamp chestnut oak	15	3
Quercus nigra	QUENIG	water oak	320	7
Quercus phellos	QUEPHE	willow oak	2	0
Quercus pumila	QUEPUM	running oak	0	1
Quercus stellata	QUESTE	post oak	180	15
Quercus virginiana	QUEVIR	live oak	1	12
Quercus velutina	QUEVEL	black oak	24	4
Family *Hamamelidaceae*				
Hamamelis virginiana	HAMVIR	American witchhazel	108	44

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App. 1, cont.   Disturbance regimes

Species	Abbreviation	Common name	C-L+fire	fire
Liquidambar styraciflua	LIQSTY	sweetgum	399	244
Family *Hypericaceae*				
Hypericum crux-andreae	HYPCRU	St. Peterswort	25	41
Hypericum hypericoides	HYPHYP	St. Andrews cross	4	33
Family *Juglandaceae*				
Carya cordiformis	CARCOR	bitternut hickory	47	16
Carya tomentosa	CARTOM	mockernut hickory	17	8
Family *Lauraceae*				
Persea borbonia	PERBOR	redbay	89	6
Sassafras albidum	SASALB	sassafras	38	3
Family *Loganiaceae*				
Gelsemium sempervirens	GELSEM	evening trumpetflower	1 181	1 585
Family *Magnoliaceae*				
Magnolia grandiflora	MAGGRA	southern magnolia	32	56
Magnolia virginiana	MAGVIR	sweetbay	43	45
Family *Myricaceae*				
Morella cerifera	MORCER	wax myrtle	426	186
Morella caroliniensis	MORCAR	southern bayberry	48	38
Family *Nyssaceae*				
Nyssa sylvatica	NYSSYL	blackgum	312	263
Family *Oleaceae*				
Chionanthus virginicus	CHIVIR	white fringetree	32	11
Fraxinus pennsylvanica	FRAPEN	green ash	8	6
Family *Pinaceae*				
Pinus echinata	PINECH	shortleaf pine	29	12
Pinus palustris	PINPAL	longleaf pine	88	129
Pinus taeda	PINTAE	loblolly pine	1 619	1 063
Family *Rhamnaceae*				
Berchemia scandens	BERSCA	Alabama supplejack	7	0
Family *Rosaceae*				
Crataegus marshallii	CRAMAR	parsley hawthorn	43	17
Crataegus spathulata	CRASPA	littlehip hawthorn	4	0
Crataegus uniflora	CRAUNI	dwarf hawthorn	6	0
Prunus serotina	PRUSER	black cherry	32	20
Prunus umbellata	PRUUMB	hog plum	21	0
Rubus spp.	RUBSPP	blackberry	18	18
Rubus trivialis	RUBTRI	southern dewberry	44	15
Family *Sapotaceae*				
Sideroxylon lanuginosum	SIDLAN	gum bully	3	0
Family *Smilacaceae*				
Smilax bona-nox	SMIBON	saw greenbrier	7	13
Smilax glauca	SMIGLA	cat greenbrier	842	728
Smilax laurifolia	SMILAU	laurel greenbrier	1	3
Smilax pumila	SMIPUM	sarsparilla-vine	241	121
Smilax rotundifolia	SMIROT	roundleaf greenbrier	238	95
Smilax smallii	SMISMA	lanceleaf greenbrier	4	4
Family *Styracaceae*				
Styrax grandifolius	STYGRA	bigleaf snowbell	239	69
Halesia diptera	HALDIP	two-wing silverbell	28	4
Family *Symplocaceae*				
Symplocos tinctoria	SYMTIN	common sweetleaf	32	36
Family *Ulmaceae*				
Celtis laevigata var. *reticulata*	CELRET	netleaf hackberry	2	0
Ulmus alata	ULMALA	winged elm	12	3
Family *Verbenaceae*				
Callicarpa americana	CALAME	American beautyberry	186	27
Family *Vitaceae*				
Parthenocissus quinquefolia	PARQUI	Virginia creeper	74	4
Vitis aestivalis	VITAES	summer grape	2	1
Vitis rotundifolia	VITROT	muscadine	237	288
Total species			81	68
Total individuals			12 677	11 414